Suitability of Some Southern and Western Pines as Hosts for the Pine Shoot Beetle, *Tomicus piniperda* (Coleoptera: Scolytidae)

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ABSTRACT The pine shoot beetle, *Tomicus piniperda* (L.), is an exotic pest that has become established in North America. Discovered in Ohio in 1992, it has since been found in at least 13 states and parts of Canada. The beetle can cause significant growth loss in pines, and it represents a potential threat to trees in areas where it has not yet become established. To evaluate this threat to native pines, field and laboratory tests were conducted on several common and important southern and western species to determine whether they are acceptable hosts for *T. piniperda*. Comparisons with *Pinus sylvestris* L., Scots pine, a preferred natural host for the beetle, were made where possible. Measurements of beetle attack success on southern pine billets showed that *Pinus taeda* L., *Pinus echinata* Miller, *Pinus elliottii* var. *elliottii* Engelmann, *Pinus palustris* Miller, and *Pinus virginiana* Miller (loblolly, shortleaf, slash, longleaf, and Virginia pine, respectively) and two western pines, *Pinus ponderosa* Lawson and *Pinus contorta* Douglas (ponderosa and lodgepole pine, respectively), were acceptable for breeding material, but brood production was highly variable. Among the southern pines, *P. taeda* and *P. echinata* were susceptible to shoot feeding by *T. piniperda*, whereas *P. elliottii* was highly resistant and *P. palustris* seemed to be virtually immune. Shoot feeding tests on the western pines were conducted only in the laboratory, but there was moderate-to-good survival of adults feeding on both species. It seems that if *T. piniperda* is introduced into the south and west it will likely establish and may cause some damage to native pines. *P. taeda* may be affected more than other southern pines because it is the most abundant species, it is readily attacked for brood production, which can result in moderately large broods, and the beetle survives well during maturation feeding on *P. taeda* shoots.

KEY WORDS *Tomicus piniperda*, pine shoot beetle, southern pines

THE PINE SHOOT BEETLE, *Tomicus piniperda* (L.) (Coleoptera: Scolytidae), was discovered attacking Scots pine, *Pinus sylvestris* L. in Lorain County, Ohio, in July 1992 (Haack and Kucera 1993, Nielsen 1993, Haack and Poland 2001). Although it had been intercepted at U.S. ports on numerous occasions (Haack et al. 1997, Haack 2001), this was the first evidence of establishment in North America. As of August 2003, the beetle has subsequently been found in 13 midwestern and northeastern states attacking Scots pine plus some native pines (Haack and Poland 2001). The native range of *T. piniperda* constitutes a significant proportion of the Paleartic region where it is considered to be a significant pest (Langstrom 1980, Ye 1991). Although much of the information regarding the bionomics of the pine shoot beetle relates to its effect on Scots pine, several other Eurasian species are attacked as are a number of North American pines introduced into Europe (Langstrom 1980). Although there are no data available on the effect of *T. piniperda* attacks on growth of native pines in North America, Czokajlo et al. (1997) found significant increment growth reduction from pine shoot beetle attacks in a 35-yr-old Scots pine plantation in New York, and Scarr et al. (1999) found pine shoot beetle-associated mortality of Scots pine in Ontario, Canada.

Unlike most scolytid bark beetles that feed exclusively on the inner bark of their hosts, the pine shoot beetle has two feeding stages. Adults emerge from overwintering sites in early spring to seek new breeding material in the form of stumps, fresh logs, and broken limbs. Vigorously growing host material is not considered to be suitable for brood production (Schroeder 1987). They do not seem to have an aggregation pheromone unlike many scolytids but instead rely on host volatiles to attract both sexes (Loyttyniemi et al. 1980). Mated females construct egg galleries within the phloem and deposit eggs along the sides of the galleries. After eclosion, larvae consume the phloem and remain beneath the bark until they pupate and subsequently emerge as adults.

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Newly emerged adults fly to nearby trees where they mine the centers of new shoots for several months, they build energy reserves, and the eggs mature in the females. Maturation feeding has been well documented in Scots pine stands in Canada (Ryall and Smith 2000) and in Scots pine Christmas tree plantations in Indiana (Kauffman et al. 1998, Haack et al. 2001) and Michigan (Haack et al. 2000, 2001). A single adult may mine several different shoots during late summer and fall. Intensive maturation feeding may cause shoot mortality and result in growth reduction or some loss of form. Additionally, seed production may be reduced when cone-bearing shoots are attacked. In colder parts of its range, decreasing daylength and freezing temperatures induce pine shoot beetle adults to seek overwintering sites in the outer bark at the base of trees near the soil line (Langstrom 1983, Petrice et al. 2002).

The pine-growing regions of the southeastern and western United States are important sources of wood and fiber. A few native pine species are grown in extensive commercial forests, often in intensively managed plantations in the southeast. The forest products industry in this region constitutes an important part of the local and national economies. If the host range of *T. piniperda* includes southern and western pine species, then the introduction of this exotic pest into these areas represents a potential significant financial and ecological threat. Pine trees are also extremely important components of many natural ecotypes throughout these regions. In natural as well as landscaped settings, pines are an integral part of the southern region and represent substantial growing stock and recreational resources in the west.

We report here studies conducted to determine whether the pine shoot beetle could use the major southern pine species and two of the common western pines as hosts. Because the pine shoot beetle has two feeding phases, it was necessary to conduct acceptance tests for both brood production within the phloem and shoot feeding (Schroeder 1988).

Materials and Methods

In 1993 and 1995, four of the most economically important, native southern pine species were tested for suitability as brood rearing and shoot feeding hosts for *T. piniperda:* loblolly pine, *Pinus taeda* L.; shortleaf pine, *Pinus echinata* Miller; slash pine, *Pinus elliottii* var. *elliottii* Engelmann; and longleaf pine, *Pinus palustris* Miller. Where possible, the southern pines were compared with Scots pine, *Pinus sylvestris* L., one of the preferred natural hosts of *T. piniperda* in Eurasia. Limited suitability tests were conducted on the native Virginia pine, *Pinus virginiana* Miller, because it is commonly grown for Christmas trees in the south. In 1995, two western species, ponderosa pine (*Pinus ponderosa* Lawson) and lodgepole pine (*Pinus contorta* Douglas), were evaluated in a similar manner.

Field Trials

1993 Brood Production Evaluations. In tests for suitability as brood rearing hosts, southern pines were felled in Georgia during February, and 1-m-long billets of each diameter class were removed from each tree. Two diameter classes of billets (10 and 20 cm) were used in the test. Billets were collected from *P. taeda*, *P. elliottii*, *P. echinata*, *P. palustris*, and *P. virginiana.* Billets of similar sizes from *P. sylvestris* were collected at the same time in Michigan and Ohio. Twelve trees of each species were sampled for this test. The billets were transported to beetle-infested Christmas tree plantations in Michigan and Ohio and placed in the field at each site in six groups (replications), which contained one small (10 ± 1 cm) and one large (20 ± 1 cm) billet of each species. The billets were placed in the field in late February and remained in place throughout the flight/attack period until early June. Billets were randomly assigned to each replicate at the two sites. Differences in attack density and brood production by site were not significant (Tukey's test; $\alpha = 0.1$; $n = 6$), and subsequent mean separation tests were conducted on pooled data from both sites.

When broods of *T. piniperda* had matured (mostly final instars and pupae), the billets were collected and taken to the Ohio Agricultural Research and Development Center (OARDC) in Wooster, OH. Billets were placed in rearing chambers constructed from plastic drums through which air was circulated to reduce the potential for decay and fermentation (Berisford et al. 1971). Emerging arthropods were collected from attached mason jars twice per week. The laboratory was maintained at ambient temperatures throughout the emergence period. When emergence was complete, the billets were removed, and any insects remaining in the cans were collected. The bark was carefully removed from each billet, and any remaining brood adults were collected and added to the rearing counts. Numbers of *T. piniperda* attacks and lengths of egg galleries were recorded, and each billet was measured (length and diameter) for subsequent calculations of surface area. Data were expressed as numbers of attacks per 1,000 cm^2 of billet surface and numbers of adults produced per linear centimeter of egg gallery on each pine species. The Tukey–Kramer multiple comparison test was used to determine significant differences ($\alpha = 0.05$; $n = 6$).

1995 Brood Production Evaluations. Following the protocol established in 1993, *P. ponderosa* and *P. contorta* were evaluated for colonization and brood production by pine shoot beetle. *P. sylvestris* was included as an internal standard. Numbers of attacks were recorded, but egg gallery length was difficult to determine due to attacks by *Ips* spp. beetles and *Pissodes* spp. weevils on the test billets. These attacks occurred much later than *Tomicus* attacks and therefore did not affect brood production. However, because the billets were peeled later than those in 1993, some galleries were obscured. Our criterion for comparison was changed to brood production per 1000 cm^2 of billet surface area (two 500-cm^2 areas evaluated), whereas attack density remained the same as in 1993 (beetles/1000 cm^2 of billet surface area). Attack density and brood production were compared for all host species at both diameter classes by analysis of variance (ANOVA) ($\alpha = 0.05$; $n = 4$) by using the Student–Newman–Keuls multiple comparison test to determine significant differences among the means (SigmaStat 2.03; SPSS Inc. 1997).

1993 Shoot Feeding Evaluations. *P. taeda, P. elliottii, P. palustris,* and *P. echinata* were evaluated for susceptibility to shoot feeding by *T. piniperda* at OARDC. There were replicates of 10, 8, 18, and 8 trees for each pine species, respectively. Potted pines 1.5–2 m in height of these species were transported from Georgia to OARDC and replanted in the spring. Due to the differing root geometry of the various species, the method of handling the trees was appropriately modified. *P. elliottii* and *P. taeda* have relatively dispersed root systems and were grown in individual containers (19-liter plastic tubs). Due to the large tap roots of *P. palustris* and *P. echinata,* individual containers were not suitable for maintaining these species in a live condition. Individuals of these species were excavated from a nursery using a hydraulic tree spade. The root balls were then covered with burlap and wire for transport. Just before emergence of pine shoot beetle adults, the pines were enclosed in a whole-tree metal frame cage, which was then covered with white nylon fabric. This fabric allowed the potted pines to photosynthesize at close to ambient air temperature. Eight newly emerged adult beetles were then added to each cage so that beetles could select shoots for maturation feeding. Near the conclusion of the field season in October, the cages were removed and the trees were assessed for shoot feeding. Each shoot was carefully examined for evidence of beetle attack and boring. Surviving and dead beetles were collected and counted.

Fat Content Studies

Measurements of stored fat from newly emerged beetles were made as an additional indicator of host quality. Insect lipids serve as an energy source, which translates to a measure of overall fitness in terms of dispersal and reproductive capacity. Lipid content has served to quantify host quality for other scolytids (Coppedge et al. 1995).

Individual beetles were weighed upon emergence, oven dried, and weighed again. The lipids from the dried beetles were then removed using the soxhelet extraction method (Atkins 1969) and weighed again, with the difference between the dry weight and the extracted dry weight being a measure of lipid content in the beetles.

Laboratory Trials

The acceptability of five southern pines, Scots pine, and two western pines to the pine shoot beetle was also evaluated in the laboratory to determine how the beetles perform at temperatures in the Georgia Piedmont. All beetle rearing and host evaluations were conducted in the forest entomology quarantine facility at the Department of Entomology, University of Georgia. The conditions within the quarantine facility were maintained at ambient temperature and daylength.

1993 Brood Production Evaluations. Caging beetles on the potential hosts tested their suitability for brood production. Evaluations were made on 1-m-long billets with the same two diameter classes used in the field evaluations. The species evaluated were *P. taeda, P. elliottii, P. palustris, P. echinata, P. virginiana,* and *P. sylvestris.* Female beetles were selected 2–4 d postemergence from field-collected overwintering sites (stumps) in Ohio. They were placed individually under half of a gelatin capsule (no. 000, Eli Lilly & Co., Indianapolis, IN), which was inserted into a shallow groove cut into the bark with a cork borer. Ten females were caged onto each billet and left for up to 3 d to allow them to initiate attacks. Females that died or failed to attempt attack after 3 d were replaced. Once a female successfully bored into a billet, a male was introduced into the capsule. These artificially infested bolts were placed within cages, and once larvae completed development, they were transferred to rearing chambers as described previously. Emerging adults were collected and counted, and billets were peeled to determine attack success and egg gallery construction. Billet length and diameter were measured for precise calculation of surface area. Brood production was expressed as numbers of adults produced per linear centimeter of egg gallery and analyzed as described previously. Attack density data were not analyzed because number of attacks was held constant.

1993 Shoot Feeding Evaluations. Single 35–40-cm-long shoots of either *P. echinata, P. elliottii, P. taeda,* or *P. palustris* were placed in individual feeding cages consisting of quart-size plastic drinking cups covered with Saran screening (SI Corp., PTG Division, Gainesville, GA). Shoots were maintained in the cages by placing the freshly severed ends in water. Individual beetles were placed within the shoot cages, and the acceptability of the hosts was determined by the ability of the beetles to shoot feed. Shoots were maintained for 3 wk and then removed and evaluated for attack success. An attack was deemed successful if 1 cm or more of the shoot had been mined.

1995 Shoot Feeding Evaluations. Shoot feeding trials similar to the 1993 evaluations were conducted with *P. ponderosa, P. contorta,* and *P. taeda.* The primary criterion for evaluation again was percentage of successful attacks. Additionally, we weighed beetles at the onset of the trials and then again for any beetles recovered at the end of the study. The change in fresh weight in milligrams was also used to compare beetles among treatments. Results were analyzed as before using ANOVA with all pairwise comparisons made with the Student–Newman–Keuls procedure (SigmaStat version 2.03; SPSS Inc. 1997).

Results

Field Trials

1993 Brood Production Evaluations. Every billet of all pine species placed in the field was attacked by *T. piniperda.* Attack densities per 1,000 cm^2 of surface area of the pine species evaluated are shown in Fig. 1. Attacks ranged from 2.8 to 5.2 beetle incursions per 1,000 cm^2 of bolt surface area. *P. echinata* had significantly fewer attacks than *P. taeda, P. virginiana,* and *P. sylvestris.* There were no other significant differences among the other four species, although *P. elliottii* and *P. palustris* tended to have fewer attacks than *P. taeda, P. virginiana,* and *P. sylvestris* (Fig. 1).

Figure 2 shows brood production from billets attacked in the field, expressed as numbers of beetles per linear centimeter of egg gallery. The majority of the species and size classes tested fell within the same range of brood production. However, brood production was generally higher in the 20-cm-diameter class, probably due to thicker phloem (Haack et al. 1987). The larger size class of the natural host, *P. sylvestris,* produced broods that were significantly larger than any other pine species or size class tested (Fig. 2).

1995 Brood Production Evaluations. Attack densities on billets in the field were similar for *P. ponderosa* and *P. sylvestris* but significantly less for *P. contorta* (Fig. 3). Attack densities ranged from a low of 1.4 for *P. contorta* to 6.5 per 1,000 cm^2 for large-diameter *P. sylvestris* billets. This range of attack densities is consistent with results obtained in 1993. Brood production per unit of bark surface area followed a pattern similar to attack densities. The natural host, *P. sylvestris,* had significantly higher production than *P. contorta* with *P. ponderosa* being intermediate (Fig. 4). Brood densities ranged from 30 brood adults per 1,000 cm^2 for *P. contorta* to 150 per 1,000 cm^2 for *P. sylvestris. P. ponderosa* was intermediate at 90 beetles per 1,000 cm^2.

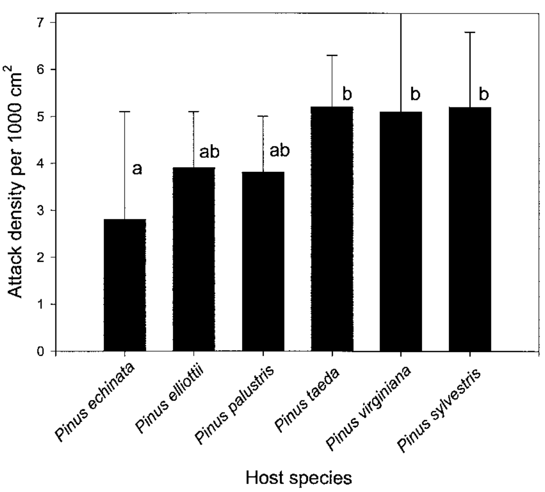

Fig. 1. Field attack densities by *T. piniperda* on five species of southern pine and Scots pine, 1993 (bars with different letters are significantly different; a = 0.05).

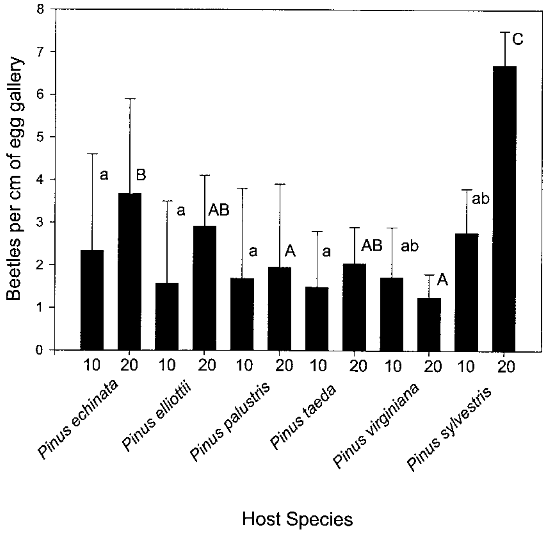

Fig. 2. *T. piniperda* brood production on field-attacked billets (10 and 20 cm in diameter) of five southern pines and Scots pine, 1993 (bars with different letters within size class are significantly different; a = 0.05).

1993 Shoot Feeding Trials. Trees on which beetles had been caged during the summer and early fall were evaluated in October before adult movement to overwintering sites. Figure 5 shows the mean numbers of beetles remaining per tree and their relative success rates on the four major southern pines. Only one beetle (dead) of the initial 144 caged onto *P. palustris* was located. There were no successful entries into longleaf pine shoots, but there was evidence of chewing on needle bases on a single shoot where the only beetle was found. The beetles made many attempts to attack *P. elliottii,* but all were unsuccessful. Nearly one-half of the introduced beetles were located, but they were all dead. Most of the beetles had apparently

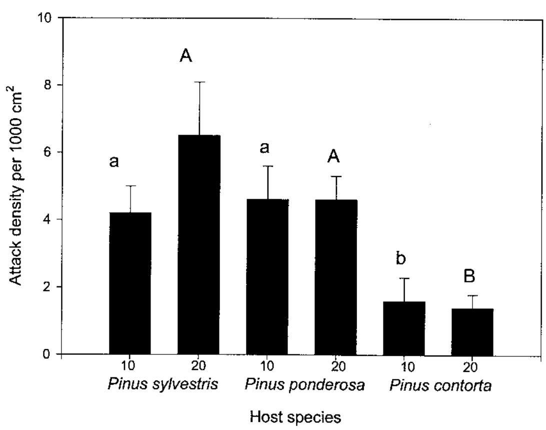

Fig. 3. Field attack densities by *T. piniperda* on 10- and 20-cm-diameter billets of two western pines and loblolly pine, 1995 (bars with different letters within a size class are significantly different; a = 0.05).

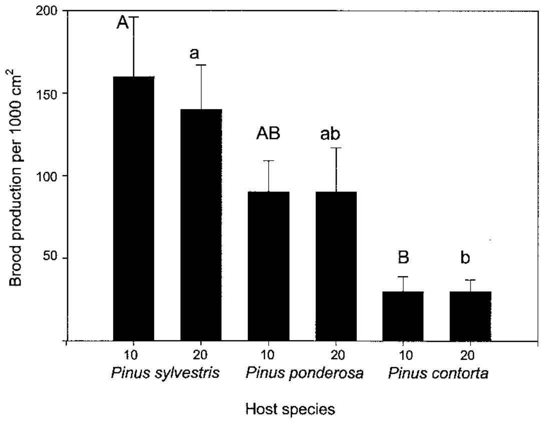

Fig. 4. *T. piniperda* brood production on field-attacked billets (10 and 20 cm in diameter) of two western pines and loblolly pine, 1995 (bars with different letters within a size class are significantly different; a = 0.05).

died as the result of "pitchout" similar to that manifested by trees resisting bark beetle attacks along their trunks. *P. echinata* had about one successful attack per tree and a few live beetles were found. There was also evidence of unsuccessful attacks on *P. echinata. P. taeda* seemed to be the best host for shoot feeding among the southern pines. There were approximately three successful attacks per tree, and most of the beetles located were alive and feeding within the shoots. There were a few unsuccessful attacks on *P. taeda* as well (Fig. 5).

Laboratory Trials

1993 Brood Production Evaluations. Fig. 6 shows pine shoot beetle brood production per linear centimeter of egg gallery resulting from forced attacks in

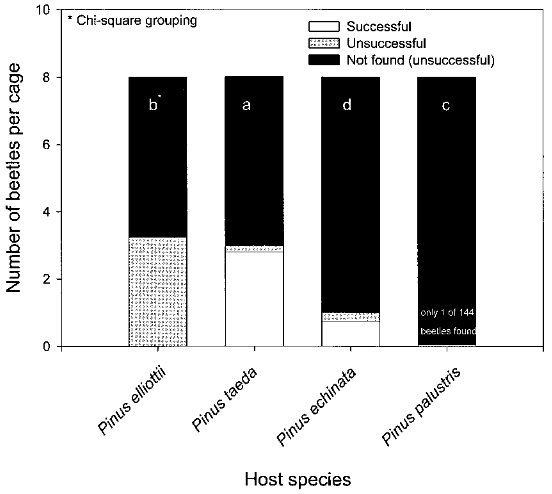

Fig. 5. Shoot feeding by *T. piniperda* on caged southern pines in the field, 1993 (bars with different letters are significantly different; a = 0.05).

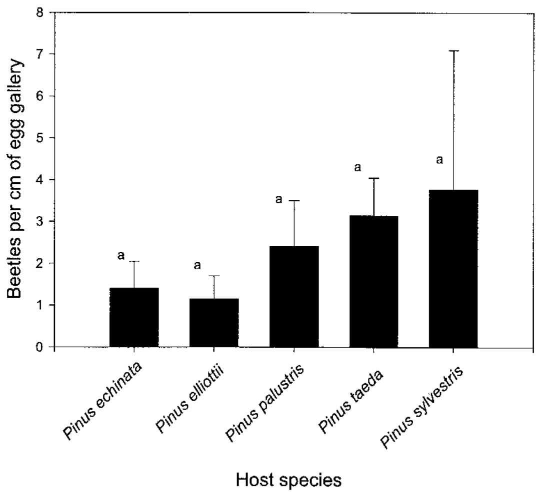

Fig. 6. *T. piniperda* brood production on four southern pines and Scots pine in the laboratory, 1993 (bars with different letters are significantly different; a = 0.05).

the laboratory. Because the goal of this portion of the experiment was to produce a series of artificially infested bolts, the number of attempts for each of the species tested was not equal. In all cases, the failure of an attack was followed by another attempt. Thus, hosts upon which attacks were most successful had fewer attempts than those on which initial attacks failed. Brood production in these laboratory tests was generally lower than in the field, even though attack density was too low to produce any competition among larvae for phloem. Brood production in the laboratory was more variable than in the field. Consequently, although mean brood production was different for various hosts and the highest production was on *P. sylvestris,* there were no statistically significant differences (Fig. 6).

1993 Shoot Feeding. Results from laboratory evaluations on the acceptability of southern pines for shoot feeding by *T. piniperda* were similar to those found in field experiments with the exception of *P. elliottii* (Fig. 7). The beetles successfully attacked *P. taeda* and *P. echinata* shoots, and contrary to field trial results, were successful in attacking and feeding on *P. elliottii* shoots. This may have occurred due to reduced pitch flow from the severed shoots. The beetles were unable to successfully attack shoots of *P. palustris* in the laboratory.

1995 Shoot Feeding. Trials on severed, caged shoots indicated that *P. ponderosa, P. contorta,* and *P. taeda* were suitable hosts for feeding by pine shoot beetle. *P. taeda* had the highest percentage of success followed by *P. ponderosa* then *P. contorta* (Fig. 8), although none were significantly different ($F = 3.26, P = 0.056$ at a = 0.05). Numbers of beetles were low for *P. taeda* ($n = 12$) that contributed to a weak F statistic and a finding of nonsignificance. The gain in fresh weight by beetles recovered from shoots of these hosts was significantly different (Fig. 8) with greater weight

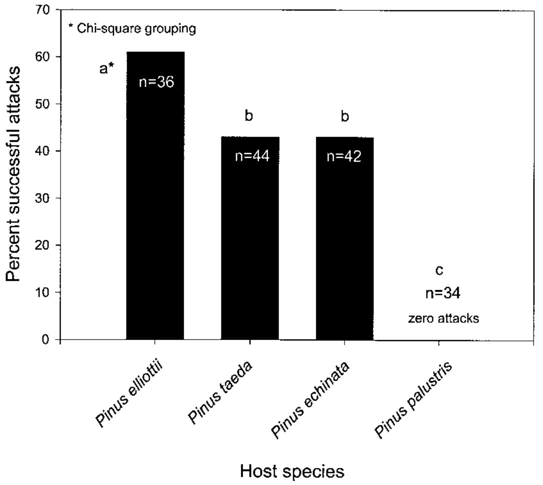

Fig. 7. Shoot feeding by *T. piniperda* on four southern pines in the laboratory, 1993 (bars with different letters significantly different; a = 0.05).

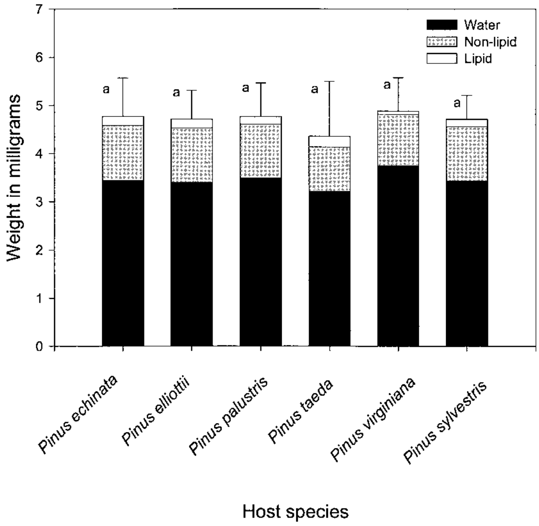

Fig. 9. Lipid content as a fitness indicator of *T. piniperda* reared on five southern pines and Scots pine, 1993 (bars with different letters are significantly different; a = 0.05).

gains on *P. taeda* (21 mg) versus 12 and 7 mg for *P. ponderosa* and *P. contorta*, respectively. The mean initial starting weights for beetles on all potential hosts were not statistically different.

Fat Content Studies. The fat content of beetles that had developed in southern pines and Scots pine are shown in Fig. 9. There were few differences among beetles, regardless of their larval host in weight and constituents of weight. The Tukey–Kramer multiple comparison statistic resulted in no significant differences in either the total weight or constituents of weight. These results suggest that if the beetle can successfully complete development, there is little difference in beetle quality from different tree hosts. Therefore, host quality might best be evaluated by numbers of brood produced rather than by fitness measures on individuals.

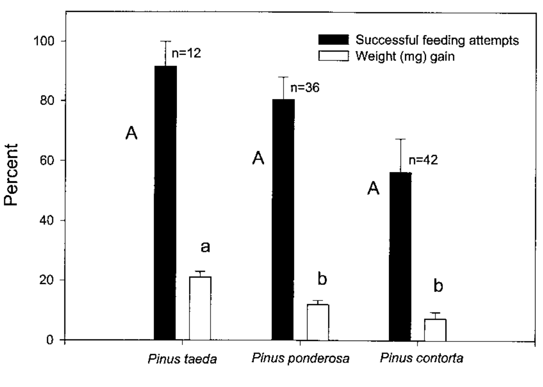

Fig. 8. Shoot feeding and fresh weight gain by *T. piniperda* on two western pines and loblolly pine, 1995 (bars with different letters are significantly different; a = 0.05).

Discussion

These studies show that *T. piniperda* can use at least five southern and two western pine species for brood production. However, shoot feeding success varied considerably, and the beetle was less successful on these potential hosts than on *P. sylvestris* as reported in the literature. Haack et al. (2000) reported that 44–75% of newly attacked shoots contained one or more pine shoot beetles and that *P. sylvestris* Christmas trees at a Michigan site averaged 3.2–6.4 attacked shoots per tree from June through August. In another study on *P. sylvestris* Christmas trees in Indiana, Haack et al. (2001) reported one to seven beetle mines per shoot with 0.1–1.7% of all current-year shoots attacked. They reference a similar study citing 0.2–4.8% of new shoots attacked. Kauffman et al. (1998) reported 7.4% of current year shoots damaged on two *P. sylvestris* Christmas trees in Lorain County, Indiana, and Ryall and Smith (2000) found shoot feeding by pine shoot beetle from July through September in southern Ontario with up to 5.3 shoots per tree attacked. Beetles were somewhat successful on *P. taeda*, *P. echinata*, *P. ponderosa*, and *P. contorta*. *P. elliottii* was highly resistant, and *P. palustris* seemed to be immune to attack. The mechanism of resistance is unknown but may be due to stem architecture and/or pitch flow. It seems that the pine shoot beetle represents little threat to these two pine species when it eventually becomes established in the south.

Tests of the qualitative status of beetles emerging from southern pine hosts showed that there were no significant differences in the lipid content or body weight compared with those from *P. sylvestris*. A comparison of fresh weight gain by pine shoot beetle feeding in the two western pine species and *P. taeda* indicates that *P. ponderosa* and particularly *P. contorta* may be inferior to *P. taeda* as shoot feeding hosts.

However, beetle performance on severed host shoots should be viewed cautiously due to differences in host defensive response between excised and intact pine shoots.

Beetles selected the novel host material for brood production at rates that varied only slightly among species. However, it is important to keep in mind that none of the southern pine species tested exists in large, single-species stands under natural conditions, although there are large acreages of monoculture pine plantations. Under these mixed stand conditions, a certain amount of host switching would likely occur, as observed by the lack of host discrimination in our field tests.

Laboratory evaluations of brood production were somewhat variable and generally produced fewer brood than field experiments. This may be related to the lack of synchrony among the beetles, potential hosts, temperatures, and/or daylength. The laboratory tests were run using beetles reared from material infested in Ohio and Indiana that had overwintered there. The tests were initiated in late February when temperatures were much higher in Georgia than the beetle would experience under field conditions in Ohio and Indiana. In addition, the southern pine hosts had begun to break winter dormancy. These factors may have reduced the ability of the beetles to overcome host resistance or caused reduced fecundity. Although the laboratory studies showed that all of the hosts tested could produce broods of *T. piniperda*, the rate of production observed may not be representative of potential brood production in the field for southern pines in their natural environment.

Regarding shoot feeding by pine shoot beetle, a continuum of acceptability of southern and western pines may exist. Some species are highly acceptable as hosts and can serve as such throughout the entire field season (*P. echinata* and *P. taeda*). Other species, such as *P. elliottii*, may be acceptable only when predisposing factors such as drought, flooding, fire damage, or other environmental conditions reduce pitch flow. However, *P. elliottii* may not be suitable for the long-term maintenance of pine shoot beetle populations. *P. ponderosa* was highly acceptable but produced low fresh weight gains in shoot-feeding beetles, a trend that was even more evident in *P. contorta*. *P. palustris* seems to be completely unacceptable for shoot feeding by *T. piniperda*.

T. piniperda were able to use novel pine species as hosts and thrived under artificial experimental conditions. Their wide geographic distribution with varying climates in the Paleartic region strongly favors their potential acclimation to the southeastern United States. There is great potential for *T. piniperda* to spread from the established population in the northeast and Midwest to the south. Studies on the spread of exotic forests pests have demonstrated the increasing importance of exotic introductions in regard to forest health (Liebhold et al. 1993). Although monitoring of established populations and the federal quarantine restricting movement of pine out of generally infested areas will tend to slow the rate of spread of the beetle, the flexible and vigorous nature of *T. piniperda* will most likely allow it to establish new populations in the pine-rich environment of the south. The potential for significant damage is increased by the ready acceptance for both brood production and maturation feeding of *P. taeda*, which is the most common and valuable species planted in the south. The ultimate ecological and economic impact of the introduction and establishment of the beetle in the southern pine region can only be answered once the almost inevitable establishment occurs. However, this study has demonstrated that once established, *T. piniperda* will be able to use a range of novel hosts that will potentially allow it to be an important component of the southern pine and possibly the western pine ecosystems.

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